

Distribution and abundance of macroinvertebrates in created wetland ecosystems

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Abstract

Benthic macroinvertebrate distribution within two constructed wetlands (Olentangy River wetlands) in central Ohio was examined in relation to physical and chemical environmental factors. Macroinvertebrate data collected using Hester-Dendy colonization plates and dipnets was analyzed using a combination of appropriate diversity indices to distinguish between wetlands. A total of 26 taxa were collected between the two wetlands. Macroinvertebrates were grouped into 5 functional guilds based on their feeding mechanisms. Two-way analysis of variance tests on wetlands showed significant difference in species composition between the two wetlands. Correspondence analysis distributed the wetland sites in four different sites based on species and site scores, with axis 1 and axis 2 explaining 48% and 35% of the variance respectively. In general, of the biotic and abiotic factors examined, abiotic factors seemed to structure the macroinvertebrate assemblage in the created wetlands.

Introduction

Although invertebrates are widely recognized as key links between wetland primary production and higher trophic levels, they have received minimal attention in conceptual models of ecosystem function and classification (Good et al. 1978, Lugo et al. 1990, Mitsch and Gooselink 1993, Wheeler et al. 1995). An understanding of distribution and abundance of invertebrates, which form an integral part of wetlands, is essential in assessing functions of natural and created systems, as they contribute to litter decomposition and food web support. Numerous studies have considered biotic and abiotic factors influencing macroinvertebrate distribution among wetlands. Presence of predators (e.g., fish, crayfish, newt) is an important biotic factor in determining macroinvertebrate abundance (Mallory et al., 1994, Nyström et al., 1996, Smith et al., 1999, Zimmer et al., 2001). The two types of abiotic factors that influence macroinvertebrate distribution and abundance are a) chemical factors such as pH, dissolved oxygen (Van Someren, 1946, Pip, 1986, Vivar et al., 1996) and b) physical factors such as hydroperiod and habitat characteristics of a wetland (e.g., depth, area, vegetation). In spite of this, the distribution of macroinvertebrates within wetlands is infrequently alluded to. Recent studies have focused on the importance of macrophytes in influencing

macroinvertebrate distribution (Weatherhead and James 2001, Cheruvilil et al. 2002, Waters and Giovanni 2002), and as potential source of food and refuge from predators (Bennet and Streams, 1986, Gilbert et al., 1999). Hurley et al. (1995) found very little correlation between macroinvertebrate distribution and environmental factors such as macrophyte distribution, physical factors, or water chemistry. This study addresses the distribution of macroinvertebrates within two created wetlands in Columbus, Ohio. The objectives of this study are: a) investigating the abundance and distribution of macroinvertebrates within these two wetlands, b) determining the composition and distribution of macroinvertebrates in the wetlands, based on their feeding guilds in association to various macrophyte habitats, and c) determining if various physical and biotic characteristics (temperature, dissolved oxygen, conductivity, pH, redox, turbidity, and different vegetation types) could explain variation in macroinvertebrate abundance.

Methods

Study area

The wetlands were created 10 years ago and are part of an 18 hectare research facility at The Ohio State University. They are 1-hectare sized perched wetlands located by the Olentangy River in Columbus, Ohio that receive lower nutrient water from the adjacent river (Spieles and Mitsch 2000). Wetland 1 was planted with twelve species of typical wetland plants (*Scripus* sp., *Juncus* sp., *Schoenoplectus tabernaemontani*, etc), while Wetland 2 was left unplanted but is now dominated by cattail *Typha* spp. (Mitsch et al. 1998).

Sampling methods and design

Samples were collected from three sites at inflow, middle, and outflow regions of the two created wetlands (Figure 1). For consistency in comparing with past data, sampling sites were kept constant. Sampling was done using two popular techniques: Hester-Dendy plates and Dip-net sampling.

The Hester-Dendy trap is an assembly of nine 8 cm x 8 cm wooden plates positioned 0.75 cm apart. Each wetland was sampled at nine locations with Hester-Dendy traps that were suspended from the boardwalk on October 9, 2003 and were left undisturbed until November 6, 2003. At the end of sampling period samples were collected and stored in 70% ethanol and Rose Bengal stain in Ziploc bags for

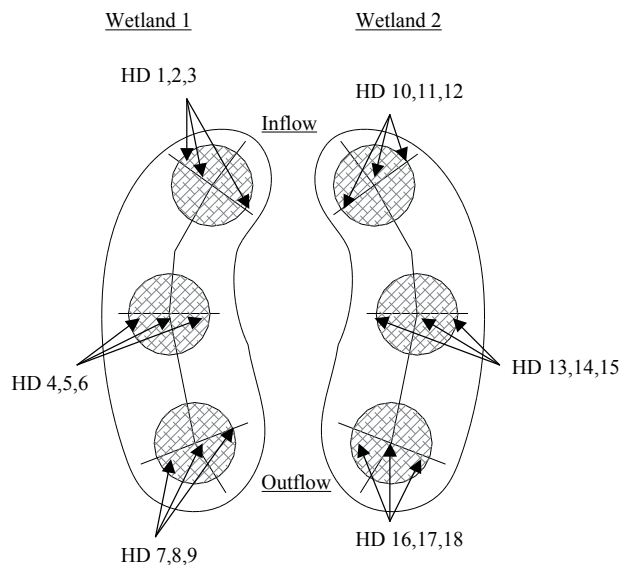


Figure 1. ORWRP experimental wetlands with locations of Hester-Dendy (HD) sampling locations.

later identification. Standardized dipnet sampling was used to quantitatively measure macroinvertebrate populations in the two wetlands. A Dipnet, with mesh size 1x1 mm, was swept back and forth for a distance of approximately one meter at least 1 cm below the bottom substrate to ensure epibenthic macroinvertebrates were included. The wetlands were sampled on alternate days from October 9, 2003 to October 27, 2003. Wetland 2 was also sampled in three different habitats consisting of three different macrophytes: *Typha angustifolia*, *Schoenoplectus tabernaemontani* and *Ludwigia palustris*, which occurred in different regions of more than 50 m² area each.

Abiotic environmental data (temperature, dissolved oxygen, pH, conductivity, turbidity, and redox) was obtained from the Olentangy Wetland Research facility.

Data analysis

Identification of samples

Macroinvertebrates were picked from plant mass and detritus and later identified up to family level using keys by McCafferty (1998), and Merritt and Cummins (1996).

Diversity indices

Shannon-Wiener index (H') is a measure of species richness in a given region (Krebs 1989). It assumes random distribution of all species in the community with equal representation. Typically values fall between 1.5 and 3.5. It is calculated using the formula

$$H' = - \sum p_i \log p_i$$

H' is the diversity index, p_i is the proportion of individuals belonging to i th species.

Species Evenness index (J) compares the diversity found in the region to the total species richness (Stiling 1999). Values for J range between 0 and 1, indicating the distribution of species through the system. The formula is

$$J = H' / H_{\max}$$

H_{\max} is the maximum diversity of species.

Renkonen index (P) is a percent similarity index to determine similar sites based on macroinvertebrate distribution. It is given by the following formula

$$P = \sum \text{minimum}(p_{1i}, p_{2i})$$

P is percentage similarity between samples 1 and 2, p_{1i} is percentage of species i in community sample 1, p_{2i} is percentage of species i in community sample 2.

Comparing two wetlands

The rank abundance of macroinvertebrates between two wetlands was done using the Hester-Dendy data. Several Two-way Analysis of Variance tests were run on dipnet data to determine the variation between and within wetlands, and within different regions of the wetlands. Dipnet data was standardized because of disproportionate size in numbers ($\log_{10} + 1$) to prevent under representation of species naturally occurring in lower numbers. Macroinvertebrate Families were grouped together based on their feeding guilds and pie charts were created for individual sites at both wetlands.

Ordination

Ordination is a collective term for multivariate techniques that arrange sites along axes on the basis of species distribution data. Correspondence analysis (CA) is a direct gradient technique to understand distribution of species along specific environmental gradients (Oksanen et al., 1988, Oksanen, 1997). CA was run on species abundance data at various sites in the wetland. The relationships of macroinvertebrate assemblage structure to environmental factors were analyzed by canonical correspondence analysis (CCA). CCA is a direct gradient analysis method that analyzes concurrently the species and environmental data and produces two types of site scores. Weighted average site scores were used in this study. CCA ordination was carried out with the CANOCO software package (Version 4.5, ter Braak, 2002).

Results

Of the 22,880 macroinvertebrates collected from the Olentangy wetlands, 7,566 were from Wetland 1 (849 on Hester-Dendy traps, and 6,717 with Dipnets), and 15,314 were from Wetland 2 (953 on Hester-Dendy traps, and 14,361 with Dipnets). Macroinvertebrates were identified to family level in most cases due to enormous numbers with a total of thirteen orders and twenty six families. Macroinvertebrate diversity from the wetlands from 1994 to 2003 is summarized in Table 1. Macroinvertebrate data from the Hester-Dendy traps for this year was log transformed and subject to a rank abundance graph that showed Oligochaetes, Gastropods, Hirudinea, and Crustaceans (Copepoda) occupied the top four positions in the community (Figure 2).

Diversity indices

Shannon-Wiener diversity and species evenness indices

are shown in Table 2. Wetland 2 at the mid-section and the *Ludwigia* sp. vegetation in Wetland 2 showed the maximum diversity with a high score of 20 on species richness. However, the inflow at Wetland 1 had the highest Shannon-Wiener index indicating higher number and abundance in species. Evenness that quantifies the unequal representation (few dominant species in relation to other relatively uncommon) against hypothetical community in which all species are equally represented, again shows higher values in the inflow regions of both the wetlands. The Renkonen index was highest ($P = .84$) for outflow and mid-section regions of Wetland 2 (Table 3). The Inflow region of Wetland 2 and mid-section region of Wetland 1 showed high similarity ($P = .80$). *Ludwigia* and bullrush habitats in Wetland 2 scored high similarity ($P = 0.82$).

Comparison of macroinvertebrate communities

A summary of macroinvertebrate diversity from previous years (1994 to 2003) in Table 1 (after Webb and Mitsch 2001) shows a higher representation of taxa during this year's sampling. Due to larger sample size, Two-way Analysis of Variance tests were performed on log transformed [$\text{Log}_{10}(x+1)$] data to check for significant differences in assemblage structure of macroinvertebrates between and within various selected sites in Olentangy river wetlands (Table 4).

As expected, the abundance of aquatic macroinvertebrates from the two wetlands was significantly different (p -value

$< .001$), although there was no significant difference in species composition. There was significant difference between inflow and outflow sites in both wetlands. Species composition between inflows in both wetlands was significantly different (p -value $< .001$), as it was for outflow sites and mid-section sites between wetlands.

Wetland 2 was sampled in three extra habitats along with the regular sample sites to observe the difference in species composition. The three different habitats were compared to the Wetland 2 data (average of inflow, mid-section, and outflow sites). The analysis showed a significant difference (p -value $< .001$) between the sites and also among the species composition. Cattail, bullrush, and *Ludwigia* habitats also showed significant differences within sites (p -value $< .001$) and in species composition (p -value = .05).

The macroinvertebrates were grouped according to their feeding mechanism (Table 5), based on Merritt and Cummins' (1996) classification, into five guilds: a) collector, b) shredder, c) scraper, d) predator, and e) piercer. Pie charts for each habitat in both wetlands were generated using percentage values of the data (Figure 3). Collectors dominated the wetlands by more than half the macroinvertebrate composition. In both the wetlands there is a distinct trend of percentage of collectors decreasing from the inflow to outflow regions. At the same time, percentage of scrapers increased from inflow to outflow regions in both wetlands. Percentage of shredders remained very low in all the sites across wetlands.

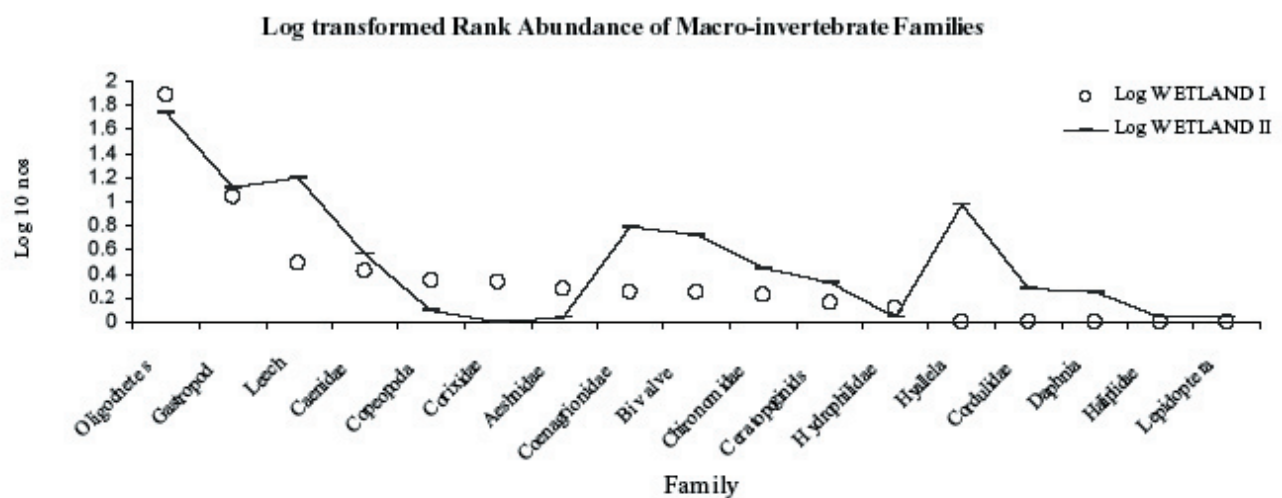


Figure 2. Rank abundance of macroinvertebrate taxa found in Wetland 1 and 2.

Table 1. Macroinvertebrate diversity at Olentangy River Wetland basins 1 and 2 from years 1994 to 2003 (continued after Acharyya and Mitsch 2001)

		1994	1995	1996	1997	1998	1999	2000	2001	2003
Class										
	Arachnida									✓
	Crustacea		✓	✓	✓		✓	✓	✓	✓
	Gastropoda	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Hirudinea					✓	✓	✓		✓
	Hymenoptera								✓	
	Insecta	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Oligochaeta					✓	✓	✓		✓
	Pelecypoda					✓	✓	✓		✓
Order										
Family										
Acariformes	Hydrocaridae		✓							✓
Arhynchobdellia	Hirudinidae					✓	✓	✓		✓
Amphipoda	Gammarus	✓	✓	✓	✓	✓	✓	✓	✓	✓
Amphipoda	Hyalloidea	✓	✓	✓	✓	✓	✓	✓	✓	✓
Cladocera	Daphnia		✓	✓	✓			✓	✓	✓
Coleoptera		✓	✓	✓		✓	✓	✓	✓	✓
Coleoptera	Dytiscidae									✓
Coleoptera	Haliplidae									✓
Coleoptera	Hydrophilidae									✓
Collembola				✓						
Diptera		✓	✓	✓	✓	✓	✓	✓	✓	✓
Diptera	Ceratopogonids									✓
Diptera	Chironomidae									✓
Diptera	Culicidae									✓
Diptera	Thaumaleidae									✓
Diptera	Tipulidae									✓
Ephemeroptera		✓	✓	✓	✓	✓		✓		✓
Ephemeroptera	Baetidae	✓	✓	✓	✓	✓	✓	✓	✓	✓
Ephemeroptera	Caenidae	✓	✓	✓	✓	✓	✓	✓	✓	✓
Ephemeroptera	Ephemerellidae	✓	✓	✓	✓	✓	✓	✓	✓	✓
Hemiptera		✓	✓	✓	✓	✓		✓	✓	✓
Hemiptera	Nepidae									✓
Hemiptera	Corixidae									✓
Lepidoptera										✓
Pelecypoda			✓							✓
Gastropoda		✓	✓	✓	✓			✓	✓	✓
Odonata		✓	✓	✓	✓	✓	✓		✓	✓
Odonata	Aeshnidae									✓
Odonata	Coenagrionidae									✓
Odonata	Cordulidae									✓
Odonata	Libellulidae									✓
Plesiopora		✓		✓	✓					✓

Table 2. Taxon diversity index and evenness within and between W1 and W2, along with three different macrophyte habitats at the Olentangy research wetlands.

	Wetland 1			Wetland 2			Cattail	Bulrush	Ludwigia
	Inlet	Middle	Outlet	Inlet	Middle	Outlet			
Sp. Richness	12	19	16	15	20	15	15	18	20
Shanon-wiener	2.80	2.57	2.00	2.76	2.40	2.46	1.85	2.67	1.07
Evenness	0.59	0.42	0.54	0.58	0.52	0.50	0.39	0.56	0.23

Table 3. Renkonen index of similarity matrix from macroinvertebrate assemblage in the Olentangy experimental wetlands.

		Wetland 1			Wetland 2					
		Inlet	Middle	Outlet	Inlet	Middle	Outlet	Cattail	Bulrush	Ludwigia
Wetland I	Inlet									
	Middle	0.75								
	Outlet	0.64	0.76							
Wetland II	Inlet	0.74	0.80	0.73						
	Middle	0.43	0.63	0.66	0.60					
	Outlet	0.52	0.68	0.69	0.69	0.84				
Wetland II	Cattail	0.35	0.25	0.32	0.36	0.47	0.40			
	Bulrush	0.44	0.40	0.35	0.47	0.54	0.49	0.72		
	Ludwigia	0.20	0.20	0.29	0.24	0.43	0.32	0.82	0.58	

Values in bold are significant P-values.

Table 4. Two-way Analysis of Variance tests within and between various sites at ORWRP experimental wetlands 1 and 2.

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
<i>Variance between Wetland 1 and 2</i>						
Species	0.22	26	0.01	1.33	0.24	1.93
Sites	0.14	1	0.14	21.99	< 0.001	4.23
Error	0.16	26	0.01			
Total	0.52	53				
<i>In Wetland 1 variance between inflow and outflow</i>						
Species	19.58	26	0.75	10.82	< 0.001	1.93
Sites	0.00	1	0.00	0.03	0.87	4.23
Error	1.81	26	0.07			
Total	21.39	53				
<i>In Wetland 2 variance between inflow and outflow</i>						
Species	17.69	26	0.68	16.99	< 0.001	1.93
Sites	0.04	1	0.04	0.97	0.33	4.23
Error	1.04	26	0.04			
Total	18.77	53				
<i>Variance at inflow between Wetland 1 & 2</i>						
Species	17.74	26	0.68	14.32	< 0.001	1.93
Sites	0.00	1	0.00	0.07	0.80	4.23
Error	1.24	26	0.05			
Total	18.98	53				
<i>Variance at outflow between Wetland 1 & 2</i>						
Species	20.03	26	0.77	17.94	< 0.001	1.93
Sites	0.04	1	0.04	1.03	0.32	4.23
Error	1.12	26	0.04			
Total	21.19	53				
<i>Variance at mid-section between Wetland 1 & 2</i>						
Species	16.99	26	0.65	6.62	< 0.001	1.93
Sites	0.00	1	0.00	0.03	0.87	4.23
Error	2.57	26	0.10			
Total	19.56	53				
<i>Variance between Wetland 2 (inflow, mid-section, and outflow average), and Cattail, Bulrush and Ludwigia habitats</i>						
Species	20.18	26	0.78	6.36	< 0.001	1.64
Sites	5.87	3	1.96	16.04	< 0.001	2.72
Error	9.51	78	0.12			
Total	35.55	107				
<i>Variance in Cattail, Bulrush and Ludwigia habitats</i>						
Species	25.77	26	0.99	14.12	< 0.001	1.71
Sites	0.46	2	0.23	3.26	0.05	3.18
Error	3.65	52	0.07			
Total	29.88	80				

Ordinations

Ordination of site species data matrix (CA) revealed four groups in each quadrant corresponding to the four sites from the wetlands (Figure 4). Leech and Baetids were outliers in the cluster. Species intolerant to stagnant water were clustered around the inflow region of the wetlands, whereas hardy species were closer to the outflow region. The plots taken from axis 1 and axis 2 explained 48.3% and 35% respectively (Table 6). Ecologically, axis 1 shows the gradient in species composition related to fresh water source. Axis 2 showed the distinction in species composition between naturally grown and artificially planted wetlands.

Environmental variables included in the CCA were: water temperature, turbidity, dissolved oxygen, pH, conductivity and redox. Of these, the most important variables describing the species composition among the study sites were redox,

and conductivity for axis 1, and turbidity, redox, and pH for axis 2 (Figure 5 and Table 7). In ecological terms, axis 1 showed gradients in species composition related to physical water parameters; species composition varied along a gradient from higher turbidity region facilitating higher redox potential in mixing water near the inflow of wetlands, to a higher dissolved oxygen region attributable to higher primary productivity near the outflow region of the wetland. Axis 2 mainly showed the difference between the two wetlands where, Wetland 2 had higher turbidity and was higher in pH than Wetland 1.

Discussion

Factors influencing macroinvertebrate assemblage structure and biomass in lentic ecosystems are water chemistry variables related to acidity or trophic conditions

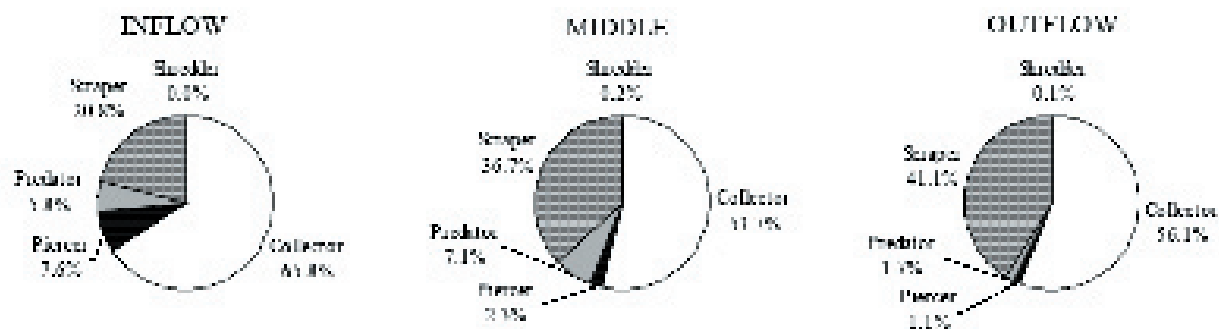
Table 5. Macroinvertebrate guild composition according to their feeding mechanism based on Merritt and Cummins's (1996) classification scheme.

Collector	Piercer	Predator	Scrapers	Shredder
<i>Baetidae</i>	<i>Mite</i>	<i>Aeshnidae</i>	<i>Gastropod</i>	<i>Haliplidae</i>
<i>Bivalve</i>	<i>Corixidae</i>	<i>Ceratopoginids</i>	<i>Thaumaleidae</i>	<i>Tipulidae</i>
<i>Caenidae</i>		<i>Coenagrionidae</i>		<i>Lepidoptera</i>
<i>Chironomidae</i>		<i>Cordulidae</i>		
<i>Copepoda</i>		<i>Dytiscidae</i>		
<i>Culicidae</i>		<i>Libellulidae</i>		
<i>Daphnia</i>		<i>Nepidae</i>		
<i>Ephemerellidae</i>				
<i>Gammarus</i>				
<i>Hyallela</i>				
<i>Hydrophilidae</i>				
<i>Leech</i>				
<i>Oligochaetes</i>				

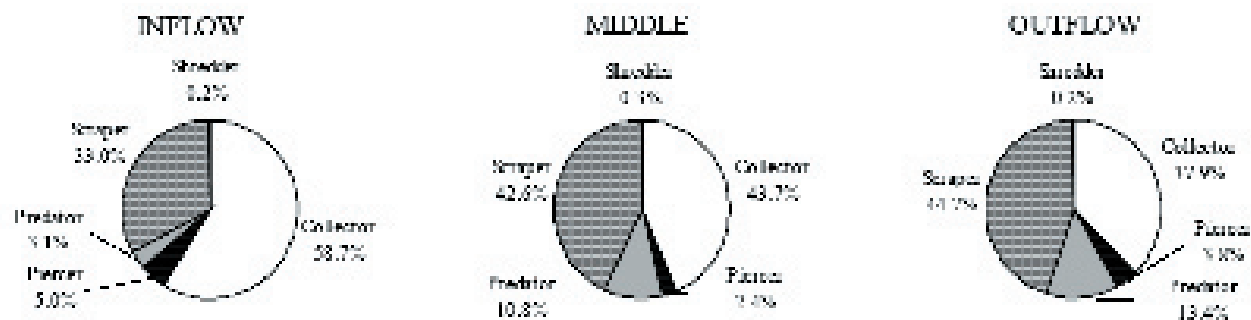
Table 6. Correspondance analysis ordinales of the macroinvertebrate assemblages of the study sites.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.135	0.098	0.046
% variance	48.33	35.03	16.64
% cumulative	48.33	83.36	100.00

a) Olentangy River Wetland Basin 1



b) Olentangy River Wetland Basin 2



c) Different macrophyte habitats in Olentangy River Wetland Basin 2

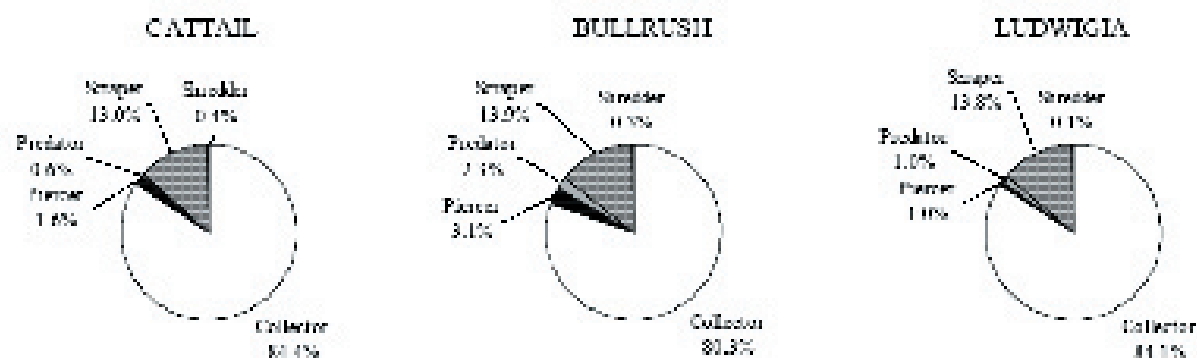


Figure 3. Macroinvertebrate grouped in five guilds based on their feeding mechanisms according to the classification of Merritt and Cummins (1996).

(Friday 1987, Rasmussen and Kalff 1987, Bordersen et al. 1998). For instance, low pH generally leads to impoverished invertebrate communities but was not an issue in the Olentangy River wetlands. Rather, redox and conductivity seemed to account for most of the variation in the composition of macroinvertebrate assemblage. According to the CCA analysis the most important individual environmental factors related to assemblage composition were redox, conductivity, turbidity and dissolved oxygen.

Small and shallow waterbodies are subject to higher temperature fluctuations (Davis et al. 2003), which may in part help explain differences in assemblage structure between the inflow region receiving fresh water and outflow region that is a stagnant water body for most part. Anoxia during winter reduces abundance and diversity of fishes in small wetlands (Tonn and Magnuson 1982, Rahel 1984) leading to changes in abundance and structure of macroinvertebrate assemblages (Wellborn et al. 1996). Lower oxygen levels

and higher macrophyte density near the inflow region in the Olentangy wetlands might result in lower abundance of fish and ducks, which might benefit invertebrates that are otherwise vulnerable to these predators. Higher abundance of oligochaetes, copepods, bivalves, and corixids near the inflow region suggests better refuge from predators. The stagnant region near the outflow of the wetlands is fairly open because of less vegetation. Higher abundance of chironomids, culicids, and gastropods suggests stagnant water body that allows higher primary productivity which is indicated by higher densities of daphnia.

Patterns in species richness

Many studies have established a positive relationship between species richness, habitat diversity and area for various taxa (Huston, 1994, Hill et al., 1994, Rosenzweig, 1995, Begon et al., 1996). Gastropods have been found to have higher diversity in larger wetlands with lush macrophyte beds as opposed to simpler water bodies (Bronmark, 1985).

Table 7. CCA ordinations of the macroinvertebrate assemblages of the ORWRP experimental wetlands.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.078	0.045	0.078
% variance	38.9	22.3	0
% cumulative	38.9	61.2	100

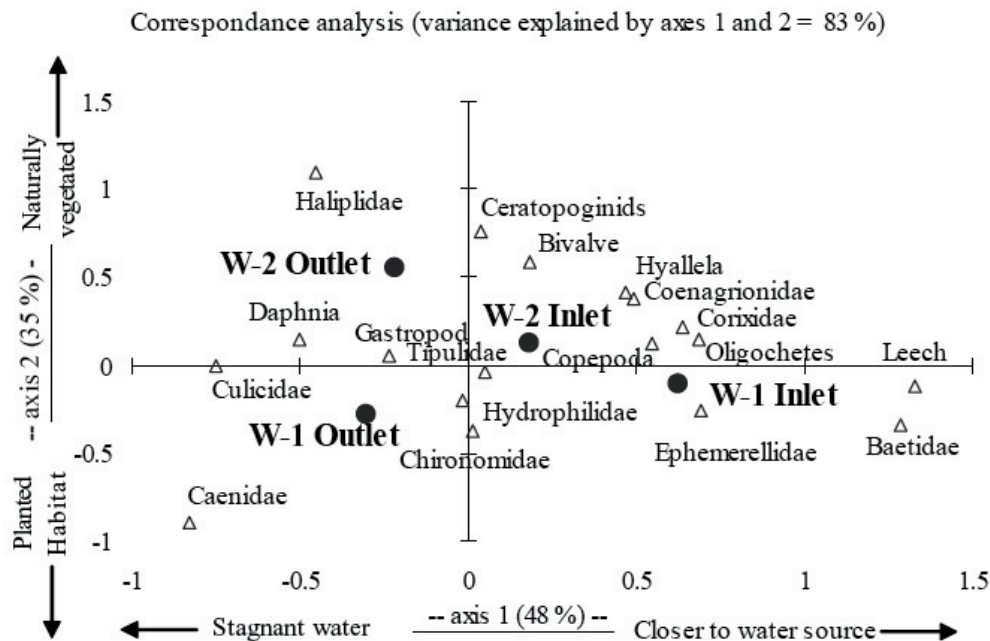


Figure 4. CA ordinations of the macroinvertebrate assemblages in the wetlands.

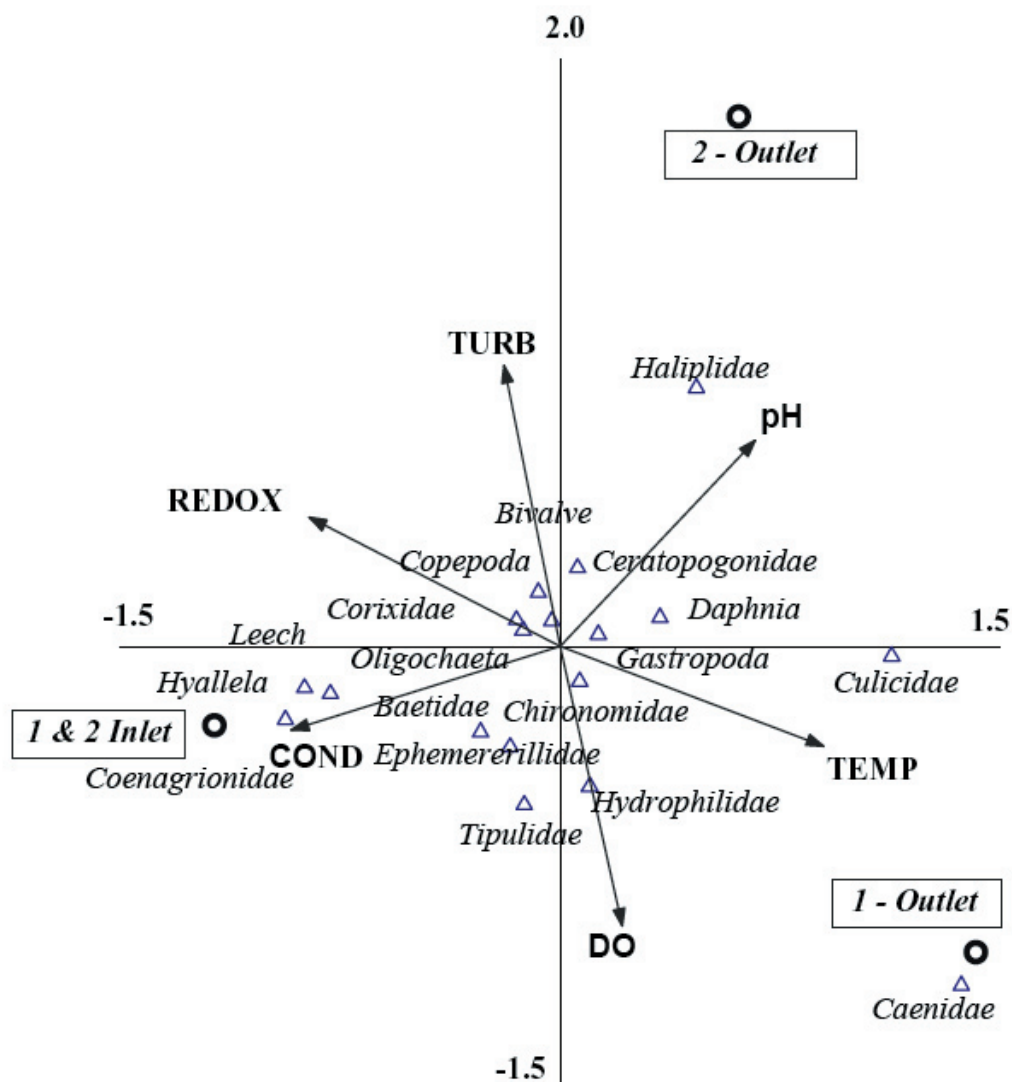


Figure 5. Species distributions along the canonical correspondence analysis axes 1 and 2.

Conversely, Nilsson et al. (1994) found dytiscid beetles to be positively related to complex structural vegetation, but negatively related to lake area. In the Olentangy wetlands, dytiscid beetles were found only in the macrophyte beds of *Ludwigia* sp. In the present study, habitat heterogeneity was positively correlated to number of macroinvertebrate species, although habitat heterogeneity explained a much higher proportion of variation in species richness. This was seemingly because of the contrasting responses in each functional feeding guilds in different wetland regions (see below), as opposed to generally positive responses to habitat heterogeneity.

Usually smaller freshwater streams receive most of their organic matter from terrestrial sources (Allan, 1995). Thus, biota adapted to use this allochthonous material responds more positively to riparian factors than within wetland environmental factors (i.e. external vs internal factors). However, shredder species richness is generally low in

bog ponds where the bottom is covered by allochthonous remains of *Sphagnum* mosses. Macroinvertebrates may be more dependent on terrestrial-based rather than aquatic-based detritus (France, 1990, 1995). Therefore, shredder richness could be expected to be higher in wetlands bordered by deciduous trees and during the latter part of autumnal leaf fall. Sampling during this part of the year would demonstrate the proper relationship of detritivorous macroinvertebrates to terrestrial yield of detritus. Percentage of shredder population in the Olentangy River wetlands is negligible due to the wetlands oligotrophic nature (Spieles and Mitsch, 2000).

Collector species richness increases with substrate particle size, which is difficult to explain as collectors prefer conditions with higher amounts of FPOM (Wallace and Webster, 1996). Similar conditions were observed in this study where higher abundance of collectors was found in regions closer to the inflow of the wetlands and lower

abundance at the outflow regions. The percentage values for the collector guild in the macrophyte habitats are an artifact of over representation of daphnia.

Scraper richness was higher in stagnant deeper waters near the outflow region of the wetlands, which would mean it was negatively affected by the amount of detritus influx from the Olentangy River at the inflow region. Similar results were found by Heino (2000) where scraper richness showed a strong positive relationship with habitat heterogeneity and water depth. Scraper richness was low in vegetated regions of *Typha angustifolia*, *Schoenoplectus tabernaemontani*, *Ludwigia palustris* habitats in the wetlands. Higher predatory species richness was found with increasing structural complexity because of macrophytes, especially in the case of dytiscid beetles (Nilsson et al. 1994). No particular trends were seen in the predatory populations at various sites in the Olentangy River wetlands. Abundance and species richness of macroinvertebrates is often positively correlated with the amount of vegetation (Carpenter and Lodge, 1986, Brown et al., 1988). So, vegetated habitats would provide more prey for invertebrate predators leading to their high density in well-developed macrophyte beds. Low water levels during the sampling period might have been a major factor for lower percentage of predator occurrence.

Conclusions

In general, differences in species composition between wetlands found at the inflow and outflow regions may have been related to the hydrology. Similarly, patterns in species richness were better explained by different macrophyte habitats than by water chemistry. The positive effects of habitat heterogeneity on resource diversity determine the total species richness. Differential influence of environmental factors on various feeding guilds suggests separate consideration of functional guilds from total species richness in macroinvertebrate assemblage studies. In conclusion, habitat structure and macrophyte types seem to be more important than water parameters in determining structure of macroinvertebrate assemblages in shallow wetlands, at least in areas that do not experience extreme physical and chemical environmental conditions.

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